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## VERTICAL DISTRIBUTION OF THE CHÆTOG-NATHA OF THE SAN DIEGO REGION IN RELATION TO THE QUESTION OF ISOLATION VS. COINCIDENCE

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#### Introduction

EVER since Jordan ('05) called attention to the almost universal neglect of Moritz Wagner's contention that geographical isolation is an important factor in the formation of species, "Jordan's Law" ('05, p. 547) that "given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort," has been subject to much controversy and diversity of opinion. The conclusions of those biologists dealing with land fauna have, as a rule, emphasized the fact of isolation. whereas those of the marine biologist have tended to emphasize the fact of coincidence, or at least to doubt the truth of isolation. It is therefore part of the business of the marine biologist, through whose investigations new and important data have been accumulated, to throw as much light as possible upon the problems of isolation and coincidence. This is particularly true with regard to data concerning the Chætognatha because, as pointed out by Kofoid ('07), the group is exclusively marine and pelagic, and so completely circumscribed as to make it probable that their entire evolution has taken place within the confines of the open sea.

At the outset, the fundamental differences in the problem with reference to land and marine fauna must be emphasized. Kofoid ('07, p. 241) has pointed out that "barriers are far less in evidence in the environment of the pelagic fauna than in that of the shore or of the land," and that, while there do exist "limited regions along the margins of great ocean currents", which might afford means of hydrographic isolation, changes in hydrographic conditions such as temperature, density, substances in solution, illumination, etc., are so gradual that stratified areas do not exist to any large extent. Furthermore, land faunas are segregated into neighboring or remote areas almost entirely with reference to latitude and longitude. With pelagic faunas this is not necessarily, perhaps not usually, the case, for a third dimension—depth—is involved. It therefore follows that closely related pelagic organisms may be coincidently distributed as regards latitude and longitude, and still be completely isolated in their vertical distribution.

This fact signifies that data respecting the isolation of a pelagic fauna will be wholly inadequate unless the vertical distribution of the particular species or group under consideration be capable of determination and analysis. In his discussion of "the coincident distribution of related species of pelagic organisms as illustrated by the Chætognatha" Kofoid ('07), while recognizing the force of this point, has utilized data pertaining almost exclusively to latitude and longitude. This was consequent upon no lack of appreciation on his part of the real problem involved, but solely to the fact that the necessary data were missing. Moreover, what little has been previously discovered relative to the vertical distribution of this group was based upon observations scattered over such large areas as to make any approach to critical analysis of the problem of isolation almost impossible. However, through the efforts of the San Diego Marine Biological Station, a mass of data has been collected which enables an entirely new light to be thrown upon this problem.

Since 1904 this station has centered its collecting upon an irregular area of about 30 square miles lying between 32° 20′ and 33° 30′ N., and between the coast and 119° W. From this small area 68,962 specimens comprising ten species of Chætognatha have been collected, and, as all depths between the surface and 350 fathoms have been examined with horizontal closing nets, the depth from which each specimen was obtained is known with the nearest approach to certainty permitted by any known method of collecting. As a critical analysis of this data has been published elsewhere [see Michael ('11) reference must be made to that paper for the methods, problems and details involved in determining the vertical distribution of each species, so that, in the following pages, only the fruits of that research bearing directly upon the present subject-matter will be discussed. It will be shown (1) that of the most closely related "couplets" of species only one has been taken from the San Diego region, (2) that, of those species occurring in this region, each has its own definite and specific manner of vertical distribution, (3) that the most diverse species (morphologically) have the most coincident vertical distribution, and (4) that, while several species have sometimes been taken in the same haul. rarely more than one was represented by sexually mature individuals

RELATIONSHIPS BETWEEN THE SPECIES OF CHÆTOGNATHA

Adopting Ritter-Záhony's ('11b) careful revision of the Chætognatha as our starting point, the group becomes separable into six genera, Sagitta, Pterosagitta, Spadella, Eukrohnia, Heterokrohnia and Krohnitta. Sagitta is represented by eighteen valid and four rather doubtful species, Pterosagitta is represented by one, Spadella by one, Eukrohnia by two, Heterokrohnia by one and Krohnitta by two.

Now the eighteen valid species of *Sagitta* fall into two sharply contrasted groups by virtue of the presence or absence of a *collarette* which is a conspicuous thickening of the epidermis posterior to the head. Ten species are

provided with this structure, while in eight it is entirely The species comprising each group are listed missing. below:

Species with Collarette Species without Collarette

S. bipunctata S. decipiens

S. neglecta S. regularis

S. ferox

S. planktonis

S. hispida (robusta Doncaster)

S. pulchra S. siboaæ

S. tenuis

S. enflata S. hexaptera

S. lyra S. qazella

S. serratodentata

 $S.\ bedoti$ S. elegans

S. macrocephala

Those species having the collarette may be further separated into diverse groups by means of the following main characteristics: (1) Those in which the body is transparent as contrasted with those in which it is opaque, (2) those in which the collarette extends to the ventral ganglion as contrasted with those in which it never extends more than half way to the ganglion, (3) those in which the anterior fin extends to the ventral ganglion as contrasted to those in which it does not, (4) those having more than 50 per cent. of the posterior fin in front of the tail-septum as contrasted with those having more than 50 per cent. of the fin behind the tail-septum, and (5) those in which the anterior fin is shorter than the posterior fin as contrasted with those in which the posterior fin is the shorter. Let it not be thought that these are the only characteristics used to differentiate the various species of Sagitta provided with the collarette. Far from it! Many others of great specific importance are made use of, but, if classified according to those just enumerated, the most closely related "couplets" remain inseparable while those species not so closely related are readily separated from each other. This may be graphically represented by arranging these five pairs of contrasted characteristics into a series of "rows" and

"columns" and then writing the names of the species, having those in question in each square made by the intersecting "arrays." Such an arrangement is given below:

TABLE I.

|  | More than 50 Per<br>Cent. of Posterior<br>Fin in Front of<br>Tail-septum | Less than 50 Per<br>Cent. of Posterior<br>Fin in Front of<br>Tail-septum | Anterior Fin<br>Shorter than<br>Posterior<br>Fin         | Anterior Fin<br>Longer than<br>Posterior<br>Fin      |
|--|--|--|--|--|
| Body transparent.  | S. bipunctata<br>S. decipiens<br>S. pulchra                              | S. tenuis  | S. bipunctata<br>S. decipiens<br>S. tenuis               | S. pulchra   |
| Body opaque.   | S. planktonis<br>S. sibogæ   | S. neglecta<br>S. regularis<br>S. ferox<br>S. hispida                    | S. neglecta<br>S. regularis<br>S. hispida                | S. planktonis<br>S. ferox<br>S. sibogæ               |
| Collarette ex-<br>tending to ven-<br>tral ganglion                       | S. planktonis  | S. neglecta<br>S. regularis<br>S. ferox                                  | S. neglecta<br>S. regularis                              | S. ferox<br>S. planktonis                            |
| Collarette not ex-<br>tending over<br>half way to ven-<br>tral ganglion. | S. bipunctata<br>S. decipiens<br>S. pulchra<br>S. sibogæ                 | S. hispida<br>S. tenuis  | S. bipunctata<br>S. decipiens<br>S. hispida<br>S. tenuis | S. pulchra<br>S. sibogæ                              |
| Anterior fin extending to ventral ganglion.                              | S. planktonis<br>S. pulchra<br>S. sibogæ                                 | S. neglecta<br>S. regularis<br>S. ferox<br>S. tenuis                     | S. neglecta<br>S. regularis<br>S. tenuis                 | S. ferox<br>S. planktonis<br>S. sibogæ<br>S. pulchræ |
| Anterior fin not extending to ganglion.                                  | S. bipunctata<br>S. decipiens  | S. hispida   | S. bipunctata<br>S. decipiens<br>S. hispida              | ·  |

An examination of this table shows that in every square where S. bipunctata occurs there also S. decipiens is found, and the same relation holds between S. neglecta and S. regularis. These four species, then, are to be regarded as constituting two very closely related "couplets." A third "couplet," whose constituent species are somewhat less closely related, is that of S. ferox and S. planktonis, which only differ in the proportional extent of the posterior fin in front of the tail-septum. The remaining species are clearly distinct.

Turning attention to those Sagitta devoid of the collarette, S. enflata, S. hexaptera, S. lyra, S. gazellæ and S. bedoti are exceedingly transparent, while S. serrato-

dentata, S. elegans and S. macrocephala are opaque. While the three opaque species are unmistakably distinct, we find that, in the transparent group, S. enflata and S. hexaptera form one closely related "couplet" while S. lyra and S. gazellæ make another. This is shown more clearly below:

TABLE II.

| P   |  |   |   |   |
|---|--|---|---|---|
|   | Posterior Fin Ex-<br>tends Caudally to<br>Seminal Vesicles | Posterior Fin<br>Never Extends to<br>Seminal Vesicles | Anterior Fin<br>Confluent with<br>Posterior Fin | Anterior and<br>Posterior Fins<br>Always Sepa-<br>rated by an<br>Interval |
| More than 50 per<br>cent. of pos-<br>terior fin in<br>front of tail-<br>septum. | S. lyra<br>S. gazellæ                                      | S. enflata<br>S. hexaptera                            | S. lyra<br>S. gazellæ                           | S. enflata<br>S. hexaptera  |
| Less than 50 per<br>cent. of pos-<br>terior fin in<br>front of tail-<br>septum. | S. bedoti  |   |   | S. bedoti   |

All told, then, we have in the genus Sagitta five closely related "couplets" of species. It is not to be presumed that every "couplet" expresses the same degree of closeness between its two members, for such is not the case. Unquestionably the two species most closely related are S. neglecta and S. regularis, and the two least so—S. ferox and S. planktonis. Now if we list these "couplets" in one column and the species so far taken from the San Diego region in another, the interesting fact is evident that, except in one case, the San Diego Sagitta contain only one species of each "couplet." Such lists are given below.

## San Diego Sagitta

 $S.\ neglecta$ 

S. bipunctata

S. lyra

S. enflata

 $S.\ hexaptera$ 

S. planktonis

S. serratodentata

### "Couplets"

S. neglecta-S. regularis

S. bipunctata-S. decipiens

S. gazellæ-S. lyra

S. enflata-S. hexaptera

 $S.\ planktonis$ - $S.\ ferox$ 

Looking to the other genera we find Eukrohnia composed of two species (E. hamata and E. fowleri), Krohnitta of two (K. subtilis and K. pacifica), and Heterokrohnia, Pterosagitta and Spadella of one each. Now E. hamata and E. fowleri form an exceedingly closely related "couplet," but only the former is known to occur in the San Diego region. Again, K. subtilis and K. pacifica are so nearly alike that it is very difficult to describe their differences although they are probably valid species. Yet, only the first has been found in California waters. Of the three remaining genera Heterokrohnia and Spadella are not represented in our collections, and Pterosagitta by only one individual of its single species P. draco.

In so far, therefore, as the relationships among the Chætognatha have been correctly interpreted, it is evident that, except for the occurrence of both *S. enflata* and *S. hexaptera*, there is no instance of two of the most closely related species having been taken from the San Diego region.

#### GENERAL DISTRIBUTION OF THE "COUPLETS"

Having pointed out that only one of a "couplet" of the most closely related species occurs in the San Diego region, it will be interesting to ascertain to what extent the same relation holds in other parts of the world. Furthermore, wherever both members of a "couplet" are recorded from the same vicinity it will be to the point to determine, if possible, to what extent their distribution within the area is coincident or isolated.

#### S. NEGLECTA AND S. REGULARIS

The members of this "couplet" may be designated as warm water, epiplanktonic species whose northern and southern limits of distribution are 35° N. and 9° S. The highest surface temperature recorded in connection with their capture is 29° C. and the lowest 15°.5 C. They were both originally described by Aida ('97) from Misaki

Harbor, where, so far as known, they are coincidently distributed.

In the Siboga area Fowler ('06) records 45 surface hauls containing either one or the other species. Of these, 35 contained S. neglecta but not S. regularis, and 6 contained S. regularis but not S. neglecta. In only 4 hauls were both species obtained. When we remember the large area covered by this expedition these results point toward contiguous and slightly overlapping, rather than coincident distribution.

The two expeditions of the Pola to the Red Sea obtained both S. neglecta and S. regularis. The collections of the first expedition (1895/96) were made in an area limited by 21° 27′ and 29° 45′ N., and 32° 30′ and 38° 30′ E., while those of the second (1897/98) were made somewhat further south and east within the limits of 15° 1' and 28° 42′ N., and 32° 56′ and 42° 31′ E. Ritter-Záhony ('09) records 32 surface hauls made during the first expedition that contained one or other of the two species. Of these, 25 contained only S. regularis, 6 only S. neglecta, while in but one haul were both species taken. During the second expedition 27 surface hauls were made of which 12 contained S. neglecta only, 10 S. regularis only, and 5 contained both. These data strongly suggest that the two species are distributed in contiguous regions which overlap considerably along the edges.

Of the other expeditions, the Biscayan, Plankton and National failed to catch either species. The Gauss obtained both in the region of Port Natal, but never in the same hauls. Doncaster ('02) records both under the names of S. septata and S. bedfordii from the Maldive and Laccadive Archipelagoes, but nothing is stated as to whether they were obtained in the same hauls or not. Ritter-Záhony ('10a) records S. regularis from Sharks Bay, Australia, but failed to find S. neglecta.

#### S. BIPUNCTATA AND S. DECIPIENS

S. bipunctata is a eurythermal, euryhyaline and cosmopolitan species recorded from the epiplankton of the arctic, sub-arctic, north temperate, tropical and south temperate Atlantic Ocean, the south temperate and tropical Indo-Australian Ocean, and the north temperate Pacific Ocean, as well as from the mesoplankton of the north temperate and tropical Atlantic. Its northern limit is 74° N. and its southern 28° S. The highest temperature recorded in connection with its capture is 33°.6 °C., while the lowest is 0°.2 °C. S. decipiens, on the other hand, is mesoplanktonic. Both were taken from the Bay of Biscay, S. decipiens from between 100 and 200 fathoms, and S. bipunctata only in open vertical hauls made between 50 and 200 fathoms to the surface. the total vield being only 7 specimens. Ritter-Záhony ('10 b, p. 4) records both from the Irish Sea, but, in regard to S. decipiens, says: "S. decipiens is purely mesoplanktonic and in the Irish area was only found at depths varying from 164 to 1,150 fathoms." Concerning S. bipunctata he says that it is "confined to the epiplankton. ... The quantity of S. bipunctata in the upper epiplankton is larger than in the lower." Finally, both species have been taken in the Atlantic Ocean between 60° N. and 8° S. but, while S. decipiens occurred only in open nets from below 100 fathoms and in closing nets from between 100 and 600 fathoms, S. bipunctata occurred only in the epiplankton. From this evidence it seems that wherever the two species occur in the same region they are isolated by their manner of vertical distribution.

#### S. LYRA AND S. GAZELLÆ

S. lyra is a cold water, nearly eurythermal species ranging from 73° N. to 7° 33′ S., the highest temperature recorded in connection with its capture being 18°.6 C. and the lowest 1°.1 C. It has been found in the epiplankton of the arctic, sub-arctic and north temperate Atlantic, and sub-antarctic Pacific Oceans, as well as in the meso-

plankton of the sub-arctic, north temperate and tropical Atlantic, the tropical Indo-Australian and the north temperate Pacific oceans. S. gazellæ, on the other hand, is a rare form. A few specimens were first taken during the Gazelle expedition from the Indian Ocean (43° S.) from a depth of 75 and 1,300 fathoms. It is also recorded from the Atlantic Ocean (35°.5 S.), where it was taken in a single haul from about 1,400 fathoms, and from the Antarctic Ocean between 60° and 66° S., where it was taken from 10, 25 and 50 fathoms. These data indicate that S. gazellæ is confined to the southern hemisphere and tends to be distributed circumpolarly. Records of the Gauss expedition show that out of 88 hauls containing either S. lyra or S. gazellæ, 39 contained only the former, 42 only the latter, and 7 both species.

#### S. ENFLATA AND S. HEXAPTERA

S. enflata is a warm water purely epiplanktonic species whose northern and southern limits of distribution are 40° 24′ N. and 34° 52′ S. The highest temperature recorded in connection with its capture is 32° C. and the lowest 15°.5 °C. It has been taken from the north temperate, tropical and south temperate Atlantic, the south temperate and tropical Indo-Australian and the north temperate Pacific oceans. S. hexaptera, on the other hand, is a eurythermal, nearly cosmopolitan species found in the lower epiplankton or mesoplankton of the arctic, sub-arctic, north temperate, tropical and south temperate Atlantic, the south temperate and tropical Indo-Australian and the north temperate and sub-antarctic Pacific oceans. Its northern and southern limits of distribution are 74° N. and 28° S., while the extremes of temperature recorded in connection with its capture are  $29^{\circ}$  C. and  $6^{\circ}$  C.

Both species have been taken together from the same areas during a number of expeditions. In the Siboga area Fowler ('06) records 58 surface hauls containing one or other of the species, of which 31 contained both,

while 26 contained S. enflata but not S. hexaptera, and only one contained S. hexaptera alone. During the first expedition of the Pola to the Red Sea 32 surface hauls were made which contained both species, 21 which contained S. enflata but not S. hexaptera, and only one which contained S. hexaptera alone. During the second expedition not a single S. hexaptera was taken in surface hauls that was not accompanied by S. enflata, there being 13 hauls containing both and 29 containing S. enflata alone. Finally, during several expeditions covering parts of the Adriatic, Ionian and Ægean seas, Ritter-Záhony ('08) records 45 surface hauls containing S. enflata, of which 6 also contained S. hexaptera, and only 4 hauls in which the latter species was taken without the former.

These data certainly indicate a high degree of coincidence. However, the fact that S. enflata is rarely reported other than from the upper epiplankton and that S. hexaptera is more typical of the lower epiplankton and mesoplankton, suggests isolation with respect to sexual maturity. Concerning this Ritter-Záhony ('10b), who has been very careful to distinguish immature from mature specimens, says: "Like S. serratodentata, S. hexaptera is a species which can not endure low temperatures until it has reached the adult stage. . . . We do not, as a rule, find large specimens until we come to the lower epiplankton." Until more is known regarding the stages of growth of these specimens taken on the surface together with S. enflata we can not regard the cases of coincidence revealed above as anything more than negative evidence of isolation.

#### S. PLANKTONIS AND S. FEROX

S. planktonis is a eurythermal species recorded from both epi- and meso-plankton of the north temperate Atlantic and Pacific oceans. It has not been reported north of 32° 45′ N., nor south of 8° 30′ S., except for a few small specimens from the Antarctic between 65° and

66° S. Its temperature range is from 27° C. to 4°.7 C. S. ferox, on the other hand, is a warm-water species confined, so far as known, to the epiplankton of the tropical Indo-Australian region. Both species were taken during the Siboga expedition, but, while S. ferox was taken in abundance from the surface, S. planktonis was taken only from the mesoplankton. There is no record of both having been taken in the same hauls except in those made with open vertical nets.

#### E. HAMATA AND E. FOWLERI

It is still an open question in my mind whether E. fowleri is a valid species or merely a synonym for E. hamata. Ritter-Záhony ('11 b) describes certain differences, but the characters used appear indicative of variation within the species rather than of constant specific characters. If they should prove synonymous, then Eukrohnia would be represented by only one species. However, assuming their validity, then E. hamata would be distributed in the mesoplankton of the Indian, Altantic and Antarctic oceans, while E. fowleri is rarer and perhaps more cosmopolitan, occurring in the Irish sea between 200 and 1,100 fathoms, in the Bay of Biscay below 325 fathoms, in the Malay Archipelago below 460 fathoms, and rarely in the open Atlantic below 500 fathoms. It might be added that E. hamata also occurs in the epiplankton of the Arctic and Antarctic regions, while E. fowleri always remains confined to the mesoplankton. During the Plankton expedition the species were taken together in only one closing-net haul made between 500 and 600 fathoms, and only twice out of 18 open vertical hauls from a variety of depths.

#### K. SUBTILIS AND K. PACIFICA

K. subtilis is regarded as a eurythermal cosmopolitan species ranging from 60° 12′ N. to 29° 30′ S. The temperature corresponding to its capture varies from 30°.8

C. to 5°.3 C. It is reported from both epi- and mesoplankton of the north temperate and tropical Atlantic and tropical Indo-Australian oceans, as well as from the epiplankton of the south temperate Atlantic and south temperate Indo-Australian oceans and from the mesoplankton of the north temperate Pacific. K. pacifica, on the other hand, is a warm-water epiplanktonic species from the tropical Atlantic and Indo-Australian, and the north temperate Pacific oceans. Its northern limit is 35° N. and its southern 7° 30′ S. During the Siboga expedition both species were taken together in but one haul, and that one made by an open vertical net from 1,000 fathoms. This is the only instance, so far as I can ascertain, where both species have been obtained from the same area.

In summing up we find that the members of each "couplet" tend to be isolated in one way or another. S. neglecta, for instance, maintains a distribution which, while overlapping more or less, is contiguous rather than coincident with that of S. regularis. In the case of S. bipunctata and S. decipiens the data show that wherever both are taken within the same area the former is confined to the epiplankton, while the latter occurs only in the mesoplankton. With S. lyra and S. gazellæ the distribution is never coincident, but, in some instances, contiguous and overlapping. S. enflata and S. hexaptera present the most striking evidence in favor of coincidence but, even here, the chances are that only the immature of S. hexaptera occur in the upper epiplankton, so that an effective physiological isolation is probably maintained. S. planktonis and S. ferox, while they do occur together in the Siboga area, are isolated by their manner of vertical distribution, S. ferox being epiplanktonic and S. planktonis mesoplanktonic. The members of the doubtful "couplet" comprising E. hamata and E. fowleri are only rarely taken in the same net hauls, which indicates contiguous rather than coincident distribution, although this appearance may be due entirely to the fact that E. fowleri is not abundant anywhere. Finally, K. subtilis and K.

pacifica have never been taken from the same region, excepting in the case of the Siboga expedition when they were obtained together in only one haul from 1,000 fathoms to the surface.

# VERTICAL DISTRIBUTION OF THE CHÆTOGNATHA OF THE SAN DIEGO REGION

The 68,962 specimens of Chætognatha obtained from the San Diego region were distributed among the various species as follows:

| s. | bipunctata     | 51,670    |
|----|----------------|-----------|
| S. | enflata        | 10,127    |
| s. | serratodentata | $6,\!575$ |
| s. | lyra           | 271       |
| S. | neglecta       | 127       |
| E. | hamata         | 72        |
| K. | subtilis       | 50        |
| s. | planktonis     | 4.1       |
| S. | hexaptera      | 28        |
| P. | draco          | 1         |

Turning attention first to those species that must be regarded as visitants rather than residents of this region we find that S. enflata, S. neglecta, and the single specimen of P. draco were all obtained from the upper epiplankton mainly during February, 1905, when the surface temperature was 15°.5 °C. One surface haul made on the morning of February 25 obtained 3,500 S. enflata, many of which were sexually mature, 9 immature S. neglecta, and the single very immature specimen of P. draco. A second surface haul, made the same morning, contained 3,100 S. enflata (most of them sexually mature) and 75 immature S. neglecta. Six more S. enflata and 38 immature S. neglecta were obtained in a surface haul made on April 29, 1905, and a seventh S. enflata in a surface haul made on June 11, 1908. Of the remaining S. enflata, 3,507 were obtained in open vertical hauls (from ten fathoms or less) during the fall of 1904, 3,500 having been taken in one haul. The five remaining S. neglecta were also obtained in the same haul, and the 13 S. enflata, still unaccounted for, were all obtained in open vertical hauls from 45, 75, 110 and 290 fathoms.

These data indicate that these three species can not be regarded as typical of the San Diego region, and since they occur abundantly in the surface waters of more tropical seas where the temperature reaches 34° C., it seems likely that they have been carried here by currents from the warmer regions, although no such currents are known with certainty. The probability of this supposition is somewhat increased because of their reoccurrence here during the past winter after an absence of over two years.

Of the remaining species, S. bipunctata, S. serratodentata, and S. lyra are the most typical of the San Diego region. The number of each species obtained from the various depths with horizontal nets is shown in the following table:

TABLE III

TOTAL NUMBER OF SPECIMENS OBTAINED WITH THE HORIZONTAL NETS

| Depth in Fathoms | S. bipunctata | S. serratodentata | S. lyra | Number<br>of Hours of<br>Hauling |
|------------------|---------------|-------------------|---------|----------------------------------|
| 0-25             | 30,733        | 93                | 5       | 108.1                            |
| 25-75            | 275           | 106               | 20      | 11.0                             |
| 75–150           | 10            | 106               | 20      | 6.5                              |
| 150-250          | 0             | 174               | 17      | 3.1                              |
| 250-350          | 0             | 43                | 54      | 5.4                              |

This table reveals the fact that S. bipunctata was obtained in by far the greatest numbers between the surface and 25 fathoms, and that it was not taken at all below 150 fathoms. S. serratodentata, on the other hand, appeared in greatest abundance between 150 and 250 fathoms, and S. lyra between 250 and 350 fathoms. However, the mere tabulation of the number of specimens taken from the various depths does not reveal the true significance of the data, for it is obvious, from the last column, that the amount of hauling, and consequently the amount of water filtered, has varied with the depth so that the relative density or abundance in the various depths is not repre-

sented by the total number of specimens obtained. A more accurate and justifiable presentation is to express the total number of specimens obtained from each of the above depths in terms of the average number per unit of time consumed in hauling. The following table reveals this relative abundance of the three species as thus determined:

TABLE IV  $\begin{tabular}{ll} \textbf{Relative Abundance or Average Number of Specimens Obtained per 20} \\ \textbf{Hours of Hauling}^1 \end{tabular}$ 

| Depth in Fathoms         | S. bipunctata | S. serratodentata | S. lyra |
|--------------------------|---------------|-------------------|---------|
| 0–25                     | 5,685         | 17                | 1       |
| 25-75                    | 420           | 193               | 36      |
| 75–150                   | 31            | 326               | 61      |
| <b>15</b> 0–2 <b>5</b> 0 | . 0           | 1,123             | 110     |
| 250-350                  | . 0           | 159               | 200     |

It is evident that this table brings into still more striking relief the fact that S. bipunctata is most abundant between the surface and 25 fathoms, from where it decreases in abundance as the depth increases, while S. serratodentata increases from a minimum between the surface and 25 fathoms to a maximum between 150 and 250 fathoms, and S. lyra increases from a minimum near the surface to a maximum in the deepest water (250 to 350 fathoms). While it is very improbable, owing to variations in many environmental conditions affecting the abundance of the three species in the various depths, that subsequent collecting would ever result in exactly the same averages as given above—it is just as improbable that, if the hauls were distributed in approximately the same manner, with regard to such environmental conditions, as those from which the above data were derived, we should find the relative abundance much altered. Consequently it is no exaggeration to say that each of these three species has its own definite and specific manner of vertical distribution just as truly as each has its own

<sup>&</sup>lt;sup>1</sup>As relative abundance is independent of the particular unit of time selected for standardizing the data, a unit of 20 hours has been used instead of the more obvious 1 hour in order to eliminate fractions in the case of *S. lyra*.

specific morphological characteristics, and it would be quite as easy to identify the species from an analysis of data regarding its vertical distribution within an area analogous to the San Diego region as it would from the usual taxonomic descriptions.

Detection of specific differences in the vertical distribution of the remaining species is rendered more uncertain because so few specimens have been obtained. However, by taking the species one at a time, it will be seen that tendencies, at least, toward specification are revealed.

#### SAGITTA PLANKTONIS

Eliminating those catches made with open vertical nets as of little or no value in determining the depths from which specimens were obtained, we find that seven S. planktonis were taken between the surface and 150 fathoms, two between 150 and 200 fathoms, six between 200 and 250 fathoms, and eleven between 250 and 300 fathoms. If we separate those obtained with horizontal from those obtained with vertical closing nets the relative abundance of the species in these various depths may be expressed as in the following table:

TABLE V

RELATIVE ABUNDANCE OF Sagitta planktonis

| Depth in Fathoms | Horizontal Closing-Net<br>Catches Showing Number<br>of Specimens per 20 Hours<br>of Hauling | Vertical Closing-Net<br>Catches Showing Number<br>of Specimens per 500 Fath-<br>oms of Hauling |
|------------------|---|--|
| 0-150            | 1   | none   |
| 150-200          | 5   | 1  |
| 200-250          | 8   | 8  |
| 250-350          | 19  | 18   |
|                  |   |  |

This table shows that this species increases in abundance as the depth increases and reaches its maximum in the neighborhood of 300 fathoms. When we realize that approximately the same relative abundance is obtained from independent considerations of data supplied by horizontal and vertical closing nets, this conclusion is placed upon solid ground, in spite of the few specimens dealt with.

#### SAGITTA HEXAPTERA

Some indication of the relative abundance of this remaining species of *Sagitta* may be gleaned from the following table:

 $\begin{tabular}{ll} TABLE & VI \\ \hline RELATIVE & ABUNDANCE & OF & Sagitta & hexaptera \\ \hline \end{tabular}$ 

| Depth in Fathoms | Horizontal Closing-Net<br>Catches Showing Number<br>of Specimens per 100 Hours<br>of Hauling | Vertical Closing-Net<br>Catches Showing Number<br>of Specimens per 1,000 Fath-<br>oms of Hauling |
|------------------|--|--|
| 0-50             | 9  | none   |
| 50-100           | 88   | 4  |
| 100-150          | none   | 2  |
| 150 - 350        | none   | none   |

When to the evidence contained in this table we add that the species was not obtained in hauls made with open vertical nets from above 45 fathoms, the facts suggest that *S. hexaptera* maintains its maximum abundance between 50 and 100 fathoms. The number of specimens, however, is too small to afford basis for any more positive conclusion.

#### Krohnitta subtilis

Regarding this species, we find that the horizontal closing nets obtained four specimens from 200 fathoms, but none from above or below this depth. The vertical closing nets, on the other hand, obtained twelve from between 50 and 200 fathoms, 25 from between 200 and 250 fathoms, and five from between 250 and 300 fathoms. Only three were obtained by the open vertical nets and those in one haul made from 250 fathoms to the surface. The following table gives a more accurate idea of the relative abundance of this species:

TABLE VII

Relative Abundance of Krohnitta subtilis Based on Vertical Closing Net Catches

| Depth in Fathoms | Average Number of Specimens<br>per 1,000 Fathom Haul |
|------------------|--|
| 0-50             | none   |
| 50-200           | 18   |
| 200 - 250        | 63   |
| 250-300          | 20   |

The table indicates that *K. subtilis* maintains its maximum abundance between 200 and 250 fathoms, and all the data agree that it does not occur above 50 fathoms.

#### EUKROHNIA HAMATA

Two specimens of this species were taken with horizontal closing nets from 110 fathoms, two from 300 fathoms, and two from 350 fathoms. The vertical closing net obtained nine from between 25 and 50 fathoms, one from between 150 and 200 fathoms, six from between 200 and 250 fathoms, and one from between 250 and 300 fathoms. None were obtained in open vertical hauls made from above 250 fathoms. These data show that *E. hamata* is typical of the mesoplankton, and suggest that the region of maximum abundance is in the neighborhood of 250 fathoms.

The essential facts presented in this brief discussion of vertical distribution may best be summed up by classifying so far as possible the various species within the San Diego region on the basis of similarities and differences in their manner of distribution. When this attempt is made we find that a key somewhat as follows may be built up:

KEY TO THE SPECIES OF CHÆTOGNATHA OF THE SAN DIEGO REGION BASED ENTIRELY UPON FACTS OF DISTRIBUTION

| A. Species conspicuously epiplanktonic, very rarely extending to   |
|--|
| a depth of 150 fathoms   |
| AA. Species conspicuously mesoplanktonic, very rarely occurring    |
| above 100 fathomsE.  |
| B. Species confined to the upper 10 fathoms                        |
| BB. Species whose depth of maximum abundance is below ,10          |
| ${\bf fathoms} \qquad \dots \qquad C.$                             |
| C. Species occurring in large numbers and distributed from the     |
| surface to 75 fathoms, but occurring in much the greatest          |
| abundance between the surface and 25 fathomsS. bipunctata.         |
| CC. Species not occurring in large numbers, the region of greatest |
| abundance being at least below 40 fathomsS. hexaptera.             |
| D. Species occurring rarely, but in large numbers (1,000 or more   |
| per haul not being unusual)  |
| DD. Species occurring rarely and in very small numbers (more than  |

| E. Species increasing in relative abundance as the depth increases,    |
|--|
| reaching a maximum at a depth of 250 fathoms or moreF.                 |
| EE. Species increasing in relative abundance as the depth increases,   |
| but reaching a maximum between 150 and 250 fathomsG.                   |
| F. Species of relatively common occurrence above 150 fathoms. S. lyra. |
| FF. Species whose occurrence above 150 fathoms is exceedingly          |
| rareS. planktonis.   |
| G. Species never occurring above 50 fathoms                            |
| GG. Species never occurring above 25 fathomsE. hamata.                 |
| GGG. Species occurring at irregular times above 25 fathoms, and some-  |
| times avan on the surface S corrected out at a                         |

It is unnecessary to state that this key is not published for the purpose of furnishing a ready means of identifying the various species of Chætognatha. Perhaps, when all the species from the four quarters of the globe have been studied as critically in regard to their behavior and ecological relations as they have in regard to their morphology, it will be possible to construct a ready means of identification on such a basis, but at present we can do no more than point out that the key does work for the San Diego region and ascertain what this fact signifies.

Its primary significance is that species are quite as distinguishable from their manner of distribution as from their morphological characteristics. In other words, each species has its own definite and distinctive mode of behavior and each adapts itself to the hydrographic and other elements of its environment in quite as definite a way as any of the other species.

This being true, the question at once arises: To what extent are morphological differences between the species proportional to, or correlatable with, their distributional differences. Ritter ('09) has pointed out that, if "change of environment and of environed organism are wholly and inseparably linked together," one ought to be able to measure and correlate the differentials between organisms with the differentials between their environments. However, in attempting to find such a "necessary correlation" in the case of Halocynthia johnsoni, native to the San Diego region, and H. hauster, native to the Washington coast, the results were negative. It is un-

necessary to point out that this is an exceedingly important line of investigation, for, if change of environment and of environed organism are not inseparably linked together, the hypothesis of "natural selection," with its attendant hypotheses of "survival of the fittest," "struggle for existence," etc., are at stake. Ask yourself if it is not a priori impossible for any of these hypothetical factors to operate in the formation of species except on the basis of variations in structure which are more or less adapted to the conditions of existence in which an organism finds itself? Again, does not logic demand that, if isolation be a necessary cause of species formation, two similar species must occupy similar but not identical or vastly different environmental complexes, because both could not be equally adapted to the same conditions by virtue of their organic difference nor to radically different conditions by virtue of their organic similarity?

Such questions sufficiently indicate the importance of our inquiry regarding the relation between the morphological and distributional characteristics of species and in this connection the key reveals the fact that those species having the most coincident vertical distribution are those having the greatest morphological difference. In other words, when the Chætognatha of this region are classified in the usual taxonomic fashion, five groups can be distinguished, of which each group contains species having the same fundamental morphological characteristics; but, when classified according to similarities and differences in vertical distribution, the species constituting any one of the five groups are those differing from each other in fundamental distributional characteristics. We have, then, two methods of classification, one of which results in groups of similar morphological but dissimilar distributional species, while the other results in groups of dissimilar morphological distributional but similar To illustrate concretely, the groups resulting species. from each method of classification are tabulated below:

| Groups of Simila | ar Distributional Species  |         | ar Morphological Species  |
|------------------|--|---------|---|
| Group 1          | (S. enflata )S. neglecta (S. bipunctata )S. hexaptera (S. lyra )S. planktonis (S. serratodentata K. subtilis E. hamata |         | S. enflata S. hexaptera S. lyra S. bipunctata S. neglecta S. planktonis S. serratodentata K. subtilis |
| 0,10up 1         | S. neglecta  | Group 1 | $\{S.\ hexaptera$   |
| Group 2          | $(S.\ bipunctata$  |         | S. lyra   |
| Group 2          | $\ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ $   |         | S. bipunctata   |
| Group 3          | $\langle S. \ lyra$  | Group 2 | $\{S.\ neglecta$  |
| Group o          | S. $planktonis$  |         | S. planktonis   |
|                  | S. serratodentata  | Group 3 | $\{S.\ serratodentata\}$  |
| Group 4.         | $igl\{ \emph{K. subtilis} igr\}$   | Group 4 | $\{K.\ subtilis$  |
|                  | E. hamata  | Group 5 | E. hamata   |

By referring to the key (p. 35) it will be seen that S. enflata is separable from S. neglecta only by the fact that the former occurs in large numbers while the latter occurs in small numbers. These two species then constitute Group 1 of similar distributional species, but, while S. enflata falls in Group 1 of similar morphological species, S. neglecta is found in Group 2. It will therefore be worth while to see just how extensively the one species is morphologically differentiated from the other. To this end I have arranged, in the following table, some of the most striking differences between the two species.

#### TABLE VIII

DIFFERENCES DEFINED Casitta on fata AND Casitta medicata

| STRUCTURAL DIFFERENCES BETWEEN Sagitta enflata AND Sagitta neglector |   |  |  |  |
|--|---|--|--|--|
| Structures   | $Sagitta\ enflata$  | $Sagitta\ neglecta$                          |  |  |
| Collarette.  | Entirely wanting.   | Extending nearly to the ventral ganglion.    |  |  |
| Anterior fin.  | Separated from ventral<br>ganglion by an interval<br>of 17-26 per cent. of<br>total length of animal. | Extends to the ventral ganglion.             |  |  |
| Length of anterior fin.  | 7.4-15.9 per cent of total length of animal.  |  |  |  |
| Length of posterior fin.   | 12-18 per cent. of total length of animal.  | -  |  |  |
| Extent of posterior fin.   | Not more than half way from tail-septum to seminal vesicles.  | To seminal vesicles.                         |  |  |
| Per cent. of posterior fin in front of tail-septum.                  | More than 50.   | Less than 50.                                |  |  |
| Appearance of body.  | Very transparent.   | Opaque.                                      |  |  |
| Width of body.   | 7-12 per cent. of total length of animal.   | 4.2-6.4 per cent. of total length of animal. |  |  |

| Muscles.            | Weak and thin.           | Strong and thick.        |  |
|---------------------|--------------------------|--------------------------|--|
| Lateral fields.     | Very large.              | Very small.              |  |
| Length of tail.     | 16-24 per cent. of total | 26-30 per cent. of total |  |
|                     | length of animal.        | length of animal.        |  |
| External process of | At least 10 times longer | Not over 4 times longer  |  |
| vestibular ridge.   | than broad.              | than broad.              |  |

Doubtless the number of differences could be increased were we to search details, but the twelve set forth in the above table sufficiently emphasize the fact that the two species are fundamentally distinct from a morphological point of view. It would, in fact, be difficult to find any species within the genus more differentiated from S. enflata than is S. neglecta.

Looking to Group 2 of similar distributional species and referring to the key (p. 35) we find that S. bipunctata is separable from S. hexaptera only by virtue of occurring in large numbers and maintaining its maximum abundance above 25 fathoms, whereas S. hexaptera occurs in small numbers and maintains its maximum abundance below 40 fathoms. In contrast to this we find that, while S. hexaptera occurs in Group 1 of similar morphological species, S. bipunctata occurs in Group 2. The following table, therefore, reveals their most fundamental structural differences.

TABLE IX

STRUCTURAL DIFFERENCES BETWEEN Sagitta bipunctata and Sagitta

| •   | hexaptera  |   |
|---|--|---|
| Structures  | Sagitta bipunctata                                 | Sagitta hexaptera                             |
| Collarette.   | Conspicuous but not extensive.                     | Entirely wanting.                             |
| Length of body.                                     | 12-17 mm. when mature.                             | 24-55 mm. when mature.                        |
| Width of body.                                      | 5-7 per cent. of length.                           | 7.3-11 per cent. of length.                   |
| Length of anterior fin.                             | 15.9-23.7 per cent. of total length of animal.     | 8.6-11.8 per cent. of total length of animal. |
| Interval between anterior fin and ventral ganglion. | 5-9 rarely 10 per cent. of total length of animal. | -   |
| Extent of posterior fin.                            | To seminal vesicles.                               | Never to seminal vesicles.                    |
| Vestibular ridge.                                   | Provided with the usual skeletal parts.            | Without the usual skeletal parts.             |

2-3 in number.

5-7 in number.

Anterior teeth.

Posterior teeth. Seizing jaws.

12-14 in number. Without crest.

2-4 in number Provided with short massive crest.

This table shows similar and just as fundamental morphological distinctions as those found between S. enflata and S. neglecta.

Group 3 of similar distributional species is composed of S. lyra and S. planktonis, and on referring to the key (p. 36) we see that the two species are distinguishable only by the fact that S. lyra is of relatively common occurrence above 150 fathoms. However, we find that S. lyra is placed in Group 1 of similar morphological species, while S. planktonis is placed in Group 2. The following table reveals the main morphological differences between the two species.

TABLE X
STRUCTURAL DIFFERENCES BETWEEN Sagitta lyra and Sagitta planktonis

| SINCELONIN BITTINGFEED BITTINGFEED SQUARE FORMATION |                            |                            |  |  |  |
|---|----------------------------|----------------------------|--|--|--|
| Structures  | Sagitta lyr <b>a</b>       | Sagitta planktonis         |  |  |  |
| Collarette.   | Entirely wanting.          | Massive, extending to      |  |  |  |
|   |                            | ventral ganglion and       |  |  |  |
|   |                            | anterior fin.              |  |  |  |
|   | Translucent, nearly trans- | Exceptionally opaque.      |  |  |  |
| Do Jan  | parent.                    | Firm and rigid, retain-    |  |  |  |
| Body.   | Tumid, but not retaining   | ing its form almost        |  |  |  |
| · At  | its form well.             | perfectly.                 |  |  |  |
| Muscles.  | Weak and thin.             | Strong and thick.          |  |  |  |
| Length of anterior fin.                             | 31.4-44.5 per cent. of     | 18.8-27 per cent. of total |  |  |  |
|   | total length of animal.    | length of animal.          |  |  |  |
| Relation of anterior                                | Confluent.                 | Separated by an interval   |  |  |  |
| fin to posterior fin.                               |                            | of 8-11 per cent. of       |  |  |  |
|   | •                          | total length of animal.    |  |  |  |
| Extent of posterior                                 | To seminal vesicles.       | Never to seminal vesicles. |  |  |  |
| fin.  |                            |                            |  |  |  |
| Length of tail.                                     | 15.6-24.8 per cent. of to- | 24-38 per cent. of total   |  |  |  |
| •   | tal length of animal.      | length of animal.          |  |  |  |
| Lateral fields.                                     | Large.                     | Very small.                |  |  |  |
| Vestibular ridge.                                   | Skeletal parts missing.    | Skeletal parts well de-    |  |  |  |
|   |                            | veloped.                   |  |  |  |
| Posterior teeth.                                    | 3-9, rarely 10 in number.  | 11-15 in number.           |  |  |  |

Here again we find that there is no question concerning the great morphological difference between these two similar distributional species. Finally we find that Group 4 of similar distributional species consists of S. serratodentata, K. subtilis, and E. hamata, and by referring to the key (p. 36) we see that they are separable only by the fact that S. serratodentata occurs to some extent above 25 fathoms, while E. hamata never occurs above this depth, and K. subtilis never occurs above 50 fathoms. Yet, we have as members of this group three species belonging to three genera, so that there can be no question regarding their fundamental morphological difference.

In what way then do these facts answer our question: "To what extent are morphological differences between species proportional to, or correlatable with, their distributional differences?" It is obvious that the only reply permitted by our data is that there is a very definite correlation, but one that is the exact reverse of what would a priori be expected on the basis of the Darwinian theory of "natural selection"; namely, that the morphological difference between two species is inversely proportional to their distributional difference, or, to state it otherwise, the coefficient of correlation between morphological and distributional differences among species approximates closely to —1.

# RELATION BETWEEN SPECIES OBTAINED IN THE SAME HAULS WITH RESPECT TO SEXUAL MATURITY

Under this head it is proposed to briefly consider the evidence of physiological isolation or coincidence between species relative to their maturity in those cases where two or more were obtained in a single haul. It is obvious that open vertical and vertical closing net hauls do not yield data relevant to this question, for the reason that the vertical distance covered is so great (25 fathoms or more) that it is impossible to tell whether the specimens of two or more species were taken from the same depth or not. Concerning the horizontal hauls, however, this objection can not be made, and when they are examined we find that only 14 out of 148 surface hauls and 23 out of 108 closingnet hauls obtained more than one species.

TABLE XI
SURFACE HAULS THAT OBTAINED MORE THAN ONE SPECIES

| Haul<br>No. | Species Obtained  | No. of<br>Specimens<br>Obtained                 | Stage of Maturity   |
|-------------|---|---|---|
| 216         | S. bipunctata<br>S. hexaptera   | 200   | Over 50 fully mature<br>Both small and very immature.   |
| 411         | S. enflata  | 3,500<br>9<br>75<br>1                           | Over half fully mature. One nearing, but none fully mature. All small and very immature. Very immature, ovary barely visible. Very immature, ovary not visible. |
| 412         | S. enflata<br>S. hexaptera<br>S. serratodentata<br>S. bipunctata<br>S. neglecta | 3,100<br>4<br>1<br>64<br>75                     | Many fully mature. All small and very immature. Very immature, ovary barely visible. All small and immature. None even approaching maturity.                    |
| 473         | S. enflata  | 6<br>38<br>6                                    | One mature, the rest nearly so. All immature. One nearly mature, the others clearly immature.   |
| 1,416       | S. enflata<br>S. bipunctata   | $\begin{smallmatrix}1\\1,620\end{smallmatrix}$  | Nearly but not quite mature.<br>All stages, many fully mature.  |
| 1,422       | S. bipunctata<br>S. planktonis  | 9<br>1  | Several stages, one fully mature.<br>Very immature, ovaries invisible.  |
| 1,426       | S. serratodentata<br>S. bipunctata  | $\substack{10\\1,250}$                          | All small and immature.<br>All stages, many fully mature.   |
| 1,582       | S. serratodentata<br>S. bipunctata  | $\begin{array}{c} 7 \\ 600 \end{array}$         | All small and immature.<br>All stages, 25 mature or nearly so.  |
| 1,591       | S. serratodentata<br>S. bipunctata  | $\begin{array}{c} 5 \\ 200 \end{array}$         | All small and immature.<br>All stages, but mostly immature.   |
| 1,605       | S. serratodentata<br>S. bipunctata  | $\begin{array}{c} 1\\35\end{array}$             | Small and very immature.<br>Mostly immature.  |
| 1,686       | S. hexaptera<br>S. bipunctata   | $\begin{smallmatrix} 1\\1,600\end{smallmatrix}$ | Small and very immature.<br>All stages, over 200 fully mature.  |
| 1,716       | S. serratodentata<br>S. bipunctata  | $\begin{array}{c} 1 \\ 50 \end{array}$          | Small and very immature.<br>Mostly immature, one fully mature.  |
|             | S. serratodentata   | 14<br>105                                       | All small and immature.<br>All stages, some fully mature.   |
| 1,772       | S. serratodentata<br>S. bipunctata  | 1 9   | Small and immature.<br>All small, none fully mature.  |

Concerning the 14 surface hauls, the following table reveals the fact that in only one haul (1,416) were representatives of two species taken which were nearly mature, and in this case the one specimen of *S. enflata* 

did not appear to be fully mature. In every other haul only one species was represented by sexually mature individuals.

The following table, which contains data relative to hauls made with horizontal closing nets, shows no instance of two species having been taken in the same haul both of which were represented by sexually mature individuals.

The facts revealed in Tables XI and XII, when taken together with the foregoing discussion of vertical distribution, suggest that the various species reach maturity for the most part during different seasons, and that fertilization probably takes place in different strata of water according to the species. In the case of S. entlata. for instance, fertilization unquestionably takes place between the surface and ten fathoms and then only during the winter, if at all, in the San Diego region. bipunctata, on the other hand, evidence is at hand [see Michael ('11)], which space forbids presenting here, showing that the species maintains a "center of migration" between 15 and 20 fathoms, from which center the species moves up and down in response to variations in light, temperature, salinity and other factors of its environment, which facts indicate that fertilization is mainly, if not exclusively, confined to this depth of 15 to 20 fathoms. In the case of S. hexaptera only the immature have been taken above 50 fathoms, which shows that fertilization must take place below this depth. Again, only the very immature of S. serratodentata have been taken above 100 fathoms, except at night when the larger specimens ascend to 50 fathoms. Similarly with S. lyra. the larger more nearly mature specimens do not occur above 200 fathoms to any extent, and so on with the other species.

It is quite true that much more knowledge is needed concerning the vertical distribution of most of the species before positive conclusions relative to the depth at which fertilization occurs can be advanced. Were the deeper water (below 350 fathoms) thoroughly investigated, dif-

 ${\bf TABLE\ XII}$  Horizontal Closing Net Hauls that Obtained more than One Species

| Haul<br>No. | Depth<br>in Fath-<br>oms | Species Obtained                         | No. of<br>Speci-<br>mens<br>Ob-<br>tained | Stage of Maturity   |
|-------------|--------------------------|--|---|---|
| 1,873       | 5                        | S. lyra                                  | 1<br>5                                    | Small and very immature. 3 fully mature, 2 immature.  |
| 1,877       | 15                       | S. serratodentata<br>S. bipunctata       | 4<br>6                                    | All small and immature. All small and immature.   |
| 1,748       | 25                       | S. lyra                                  | 5<br>6<br>4                               | All very small and immature.  One nearly mature, the rest very immature.  Small and remote from maturity. |
| 1,761       | 25                       | S. lyra                                  | 1 1                                       | Very small and immature. Nearly but not fully mature.   |
| 1,851       | 25                       | S. serratodentata S. bipunctata          | 7 2                                       | All small and immature. Nearly but not fully mature.  |
| 1,858       | 35                       | S. serratodentata S. bipunctata          | 2<br>1                                    | Small and immature.<br>Nearly but not fully mature.   |
| 1,476       | 50                       | S. hexaptera S. bipunctata S. planktonis | 1<br>300<br>1                             | Remote from maturity. All stages, several mature. Remote from maturity.                                   |
| 1,575       | 75                       | S. serratodentata<br>S. bipunctata       | 76<br>65                                  | Mostly large and nearly mature.   |
| 1,688       | 100                      | S. lyra                                  | 4<br>4                                    | Very small and immature. One nearly mature, the rest remote from maturity.                                |
| 1,714       | 100                      | S. lyra                                  | 1<br>9                                    | Small and immature. One nearly mature, the rest small and immature.                                       |
| 1,757       | 100                      | S. lyra                                  | 1 2                                       | Large and nearly mature.  |
| 1,813       | 100                      | S. lyra                                  | $\frac{2}{12}$                            | Large but not mature. All large but none fully mature.  |
| 1,979       | 100                      | S. lyra                                  | 1<br>30                                   | Large but not mature. All stages, none fully mature.  |
| 1,927       | 125                      | S. lyra                                  | 11<br>21<br>1                             | All stages, two nearly mature. All large, none fully mature. Small and very immature.                     |
| 1,735       | 160                      | S. lyra                                  | 1<br>16                                   | Small and very immature. All large and nearly mature.   |
| 1,926       | 200                      | S. lyra                                  | 13<br>46<br>1<br>3                        | All stages, none fully mature. All stages, some nearly mature. Large but very immature. Very immature.    |

| Haul<br>No. | Depth<br>in Fath-<br>oms | Species Obtained               | No. of<br>Speci-<br>mens<br>Ob-<br>tained | Stage of Maturity   |
|-------------|--------------------------|--------------------------------|---|---|
| 1,948       | 200                      | S. lyra                        | 2<br>13                                   | Large but not mature.   |
| 1,978       | 200                      | S. lyra                        | 1<br>29<br>1                              | Large, some nearly mature.  Large but not mature.  Large and nearly mature.  Very immature. |
| 1,732       | 220                      | S. lyra                        | 1<br>13                                   | Large but immature.<br>Large and nearly mature.   |
| 1,557       | 250                      | S. lyra                        | 50  | All stages, several nearly if not fully mature.   |
|             |                          | $S.\ serratodentata$           | 24  | Large but immature.   |
| 1,729       | 250                      | S. lyra                        | 2<br>17                                   | Small and immature.<br>Large, some nearly mature.   |
| 1,550       | 350                      | S. lyra<br>S. planktonis       | 2<br>3                                    | Large but not mature. Large and nearly mature.  |
| 1,567       | 350                      | S. serratodentata<br>E. hamata | 2 2                                       | Small and immature. Large and nearly mature.  |

ferentials would undoubtedly be established between S. lyra and S. planktonis with reference to their depths of maximum abundance. Again, more extensive data relative to all depths, by increasing the number of specimens and hauls with which to deal, would enable us to split the region of 250 to 350 fathoms, for instance, and thus distinguish strata and establish specific differences within much smaller limits. However, on the basis of data already accumulated, all the evidence points toward the probability that the fertilization of each species normally takes place within the limits of its depth of maximum abundance.

### SUMMARY AND GENERAL SIGNIFICANCE OF THE DATA

In the foregoing pages the following facts relative to the question of isolation and coincidence have been revealed:

1. Of the most closely related "couplets" of species only one occurs in the San Diego region, except in the case of S. enflata and S. hexaptera, the former of which can not be regarded as resident in this vicinity.

- 2. The general distribution of each member of a "couplet" is never entirely coincident with that of the other, but varies from a contiguous and overlapping to a radically isolated distribution, according to the "couplet."
- 3. Each species occurring in the San Diego region has its own definite and specific manner of vertical distribution just as truly as it has its own specific morphological characteristics.
- 4. Those San Diego species having the most similar vertical distribution are those possessing the most distinctive morphological characteristics or, to state it otherwise, the morphological difference between species is inversely proportional to their distributional difference.
- 5. Whenever two or more species have been obtained in the same haul, never more than one was represented by sexually mature individuals.
- 6. With one or two *possible* exceptions, the mature specimens of each species occur in different strata of water.

On the basis of these facts we are forced to conclude (a) that the more closely related species of Chætognatha are isolated from each other either horizontally, vertically or by virtue of physiological differences causing fertilization to take place in different strata of water, and (b) that "Jordan's Law" is only partly true, when tested by vertical distribution, for, while the more closely related species do not inhabit the same environment, they do inhabit the most remote environments.

Aside from these obvious conclusions the primary significance of this paper is that of emphasizing the need of more exhaustive and quantitative data relative to organisms, on the one hand, and their environments, on the other, before any solid basis can be had upon which to build theories regarding the operation of isolation, adaptation, natural selection, mutation and other factors supposedly concerned in the evolution of species. The

existence of this need relative to pelagic organisms and their conditions of vertical distribution is readily recognized and our first impression may be that the extent of this particular need is exceptional, but an acquaintance with the literature on evolution shows plainly that the need is very general. Indeed, this literature is fairly bulging with evidences of mimicry, protective coloration, natural selection, etc., based upon an abundance of data concerning many organisms as well as their environments, which data, while supporting the hypotheses, rarely include any facts relative to the essentially quantitative nature of either the organisms or the environments investigated. The mere fact that this sort of data supports a hypothesis and that the logic is sound is not adequate scientific proof that the hypothesis is true, for, as Pearl ('11) and others have demonstrated, logic may carry conviction, be supported by numerous data, and still prove erroneous when the quantitative relations of the facts included in such data are considered. Therein lies the mischief of much of our a priori reasoning relative to evolution, namely, that it causes us to depend so largely upon logic that we overlook or neglect as insignificant the quantitative nature of organisms and particularly of environments. Our most urgent present need, therefore, is not so much the accumulation of additional qualitative data as it is an exhaustive and quantitative treatment of those facts now at hand.

While the biometrician and, to some extent, other students of evolution are treating their data quantitatively, the ease with which large numbers of individuals of pelagic species may be obtained without apparently diminishing the supply, gives an unusual opportunity to the marine biologist for applying quantitative methods on an extensive scale to many of the important problems of evolution. If all the planktological expeditions would join hands by publishing all the data relative to every haul (those that did not as well as those that did contain the species or group under consideration) and by recording the approximate, if not the exact, number of speci-

mens of each species obtained, instead of publishing only data relative to successful hauls and recording the species as abundant or rare, many problems now so largely discussed from hypothetical points of view could be analyzed entirely on a factual basis without involving committal to any hypothesis whatsoever. For instance, by such means it would be possible:

- 1. To measure the degree of variation in the *habits* of distribution of species.
- 2. To measure the extent of correlation between variation in the vertical distribution of species and variation in their horizontal distribution.
- 3. To measure the degree of correlation between morphological and ecological characteristics of species, and so arrive at an accurate analysis of the causes of adaptation.
- 4. To measure the *range* of adaptation accompanying the same structures.
- 5. To measure the *range* of variation in structure adapted to the same environmental conditions.
- 6. To analyze the *natural* behavior of a species without involving the necessity of first placing collected individuals under the artificial conditions of the laboratory and then reading the results, arrived at by experiment, back into their natural environment. I do not wish to minimize in the least the immense value of laboratory experiments on behavior, but, no matter how great the achievement, such experiments can not afford a reliable basis for interpreting the *natural* behavior of a species until it becomes possible to re-create nature in miniature.

While these are but a few of the problems that are urgently calling for solution, I can not help but feel that, in the foregoing pages, we have touched the fringe of a line of quantitative investigation destined to yield much of importance to the student of evolution.

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